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ANNELID DESCENT: THE ORIGIN OF METAMERISM
AND THE SIGNIFICANCE OF THE MESODERM.¹

BY EDUARD MEYER.

THE recent publication by Claus of a paper "On the Morphological and Phylogenetic Significance of the Body of the Tapeworm"² has induced me to defer no longer the long-entertained and elaborated conception of the origin of metamerism amongst Annelids, and thus amongst all segmented Bilateralia, but to communicate to my fellow-workers, provisionally at least, a general sketch of it.

Claus, in the paper quoted above, refuting the conception of the tapeworm as a colony due to strobilation, brings forward evidence that the segmented Cestode body is to be derived from a non-segmented form in which, at first, the internal organs (sexual organs) appeared in metameric sequence, and later a corresponding external segmentation was introduced. This has finally attained a maximum in the superlative individualization of pieces of the body that separate completely from it in the formation of proglottids.

In my opinion, the Annelids owe the metamerism of their bodies to a process quite analogous, which here has produced a certain, but never, indeed, a complete, individualization of the segment, and which in some cases has finally degenerated into a non-sexual reproduction by fission.

This last phenomenon, in which I can see, when occurring in the higher Metazoa, a considerable degree of degradation, is often used as an argument in favor of their hypothesis by the supporters of the doctrine that animal segmentation had its origin in budding. We should not forget, however, that reproduction by fission among the Annelids has either been observed in only such forms as have a structure implying undoubtedly not primary but degen-

¹ Translated by Dr. E. A. Andrews from the *Biologisches Centralblatt*, X., July, 1890.

² Arbeit, a. d. zool. Inst. Wien, VIII., 1889.
Amer. Nat.—December.—3.

erate simplicity of structure, or (where it occurs in the less simple members of the class) appears as the almost mechanical separation of part of the body, tending to destroy the general equilibrium by the collection of sexual products. The formation of a new head in this process can only be regarded as a phenomenon of regeneration that has been thrown back into earlier periods in consequence of the regular repetition of the process of fission from generation to generation, and that finally begins in a period when the separating part is still connected with the parent.

Moreover, if metamerism in segmented animals had originally arisen from the formation of buds, then, in the first place, the production of new segments must always take place at the extreme end of the body, or, in other words, the terminal section should be always the most recently formed metamere; and, in the second place, the entire body must consist of completely equivalent, consecutive pieces. In place of this we see, however, that the new segments arise from a formative zone anterior to the telson, that the telson belongs to the oldest part of the animal, and that all parts of the body do not correspond, since neither the cephalic lobe with the buccal zone and foregut, nor the terminal piece with the hindgut, can be compared with the metameres lying between them. If we derive the origin of metamerism from the kind of strobilation found in Acalephs, then the youngest segments follow immediately upon the first body segment, which (though occurring in the segmented Cestodes) is not at all the case in all other segmented animals from the Annelids up.

The heteronomy of prostomium, trunk segments, and telson, becomes intelligible, nay necessary, when we regard the metameres as arising from the segmentation of the trunk between the head and tail pieces,—that is, as arising in situ. How may this process have been effected in phylogeny?

The acquisitions of recent years indicate with considerable certainty that all segmented animals, omitting the Cestodes, have descended directly or indirectly from Annelids, and thus in them or in their immediate ancestors the formation of metameres had its origin. As long as these ancestors are regarded as trochospheres or medusa-like creatures (Hatschek, Kleinenberg), or if the Anne-

lids are regarded as descended from Echinoderms, as has been done (R. Wagner), we can scarcely come nearer to the solution of the above question, since we are driven to resort either to budding, strobilation, or to circumlocutions, such as "intermittently progressive processes of growth and differentiation." We will, I believe, arrive much sooner at the goal if we derive the Annelids from Planarian-like ancestors, for which the development, especially the differentiation of the mesoderm, gives ample ground.

We find in Annelids, typically, as a chief constituent of the mesoderm, the two mesoderm-bands growing forward from two pole-cells. These bands, at first solid strands, subsequently break up, in the trunk, into the paired mesodermic somites, which become hollowed out and give rise to the definitive body-cavity; this constitutes the so-called secondary mesoderm. Besides this, larvæ as well as embryos of Annelids have a "primary" mesoderm, which not only functions in the larva before the formation of the mesoderm-bands, but also furnishes a considerable part of the permanent organs. To the former category belong the various simple muscles and the excretory organs of the larva; to the latter also a number of muscles, namely, the circular muscles, the transverse muscles, the muscles of the setæ sacs, septa, and mesenteries, the special muscles of the various parts of the digestive tract, also the retro-peritoneal connective tissue whenever it is formed, and in certain cases the excretory part of the definitive nephridia, which I have called the nephridial tube. Such a state of things I have established as existing in various Polychæte larvæ, and the same may be inferred with tolerable certainty from many statements in the literature, though the interpretations there are manifoldly different. The distinction between the *primary mesoderm*, or *embryonic mesenchym*, as it might be better called, and the *secondary* or *cælotomic mesoderm*, appears most plainly when a spacious primary body-cavity occurs between the ectoderm and the entoderm, separating the parietal mesenchym next the skin from the mesoderm-band next the digestive tract. As an example of this I would cite the larva of *Psygmodranchus*.³

³See Pls. 23 and 24 in Mitth. Zool. Station Neapel, VIII., 1888. I have there called the element of the primary mesoderm "parenchyma," from consideration of the possible reference to the corresponding tissue of the Turbellarians. As, however, this designation carries with it the idea of a more compact tissue, it is thus not quite a fitting one, and so I return to the old name, "mesenchym."

At the period when the mesoderm-bands are dividing into segments the mesenchym elements have so far increased throughout the entire trunk as to fill out completely the space between ectoderm and entoderm, not occupied by those bands. At the same time a portion (subsequently the septal and mesenterial muscles) penetrates between the mesodermal segments, thus leading to the division of the mesoderm-bands. This fact is also to be observed, that the external follows the internal segmentation of the body. At this stage in development, the similarity between the mesodermal structures of the young Annelid and those of an adult Turbellarian cannot be doubted. In the latter, as in the former, we find between the skin and the intestine cell aggregates, either solid or becoming hollowed out; in the latter the sexual organs, in the former the mesoderm somites (while in both the head region remains free from such structures).⁴ The structures in Annelids and Turbellarians here compared are, in my opinion, really genetically connected. All the mesenchym structures in the Annelid, both in larval and adult stages, may be compared with quite similar structures in the parenchyma of the Turbellarian; the paired, metameric, peritoneal sacs, arising from the mesoderm somites, enclosing the body-cavity and producing the sexual products in definite areas, may be regarded as sexual follicles, with much enlarged cavities and manifoldly differentiated walls.⁵

In place of a more detailed demonstration, I will here give a preliminary sketch of my views on the phylogenetic development of the Annelid, such as I gave at the last (eighth) Congress of Naturalists, at St. Petersburg, January, 1890.

⁴In the Annelid the cephalic lobe does not possess any mesoderm segment of its own, but, as I have repeatedly convinced myself, receives its peritoneal lining from the growth of the walls of the first post-oral pair of somites,—that is, the first pair of the trunk. In this process the primitive head-cavity is completely obliterated.

⁵After Hatschek had expressed the idea that "the secondary body-cavity is comparable to the cavity of the sexual glands in lower forms," R. S. Berg endeavored to derive the peritoneal segment cavities of Annelids from the sexual follicles of the Nemerteans, but soon completely renounced this "working hypothesis" in favor of Kleinenberg's recent interpretation of the mesoderm. I had conceived, in the main, the views here presented before the publication of this opinion of Berg's, and have as yet learned no valid reason for changing my mind.

I imagine the ancestors of Annelids to have been powerful, predatory Turbellarians, which lived a pelagic life, and were at that time masters of the seas. By their agility in swimming and in catching their prey these forms were distinguished from their present non-parasitic relatives, the Planarians; and only such acquirements could, in my opinion, have led to a perfection of organization in an ascending direction. The Planarians were forced to the sea bottom to take refuge amongst rocks and plants, first by these ancestors, then by their favored younger relatives, the Annelids, and finally by fish and other predatory marine animals. Here they led a creeping life, and thence gradually acquired a flat, broad body, with irregular arrangement of the internal organs. The ancestors had an elongated body, rounded in section and very supple; so that these may have borne a resemblance to the Nemerteans. Yet the Annelids cannot be derived from these worms, since they undoubtedly form a side branch, subsequently much changed and distinguished by peculiar characters (proboscis, vascular system, excretory organs). Yet these have preserved some of the internal organization derived from those common pelagic ancestors, which may give us very valuable hints in considering the Annelid body.

In the body parenchyma, partly surrounded by, partly penetrated by powerful muscle systems, were the sexual glands, appearing originally in the immature state as a single pair of compact cell-bands, but in the mature condition as long, hollow tubes, opening externally at the posterior end of the body by a pair of simple dermal pores. It is conceivable that these organs, being distended with eggs or sperm at certain times, would much interfere with the flexibility of the entire body. Now, however, in consequence of this very rigidity produced by the excessive accumulation of sexual products, they would finally yield to the constantly repeated endeavors of the animal to regain its accustomed mobility, and divide up into smaller glands. Thus it would have been the serpentine swimming motions (by which alone we can imagine the rapid change of place of a long worm in the water) of the Turbellarian-like ancestors of the Annelids which caused the disintegration of the two originally uniform, elonga-

ted genital tubes into two rows of equal segments. In this process, very probably, certain muscular regions, especially those parts of the transverse and dorso-ventral systems serving in that mode of motion, took active part during their contraction by continually constricting the undivided genital glands.

The series of successive sexual glands thus arising, and arranged symmetrically on both sides of the intestinal canal for the maintenance of equilibrium, now furnished internal metameric centres, about which the remaining organs, which were previously diffusely distributed in and on the body, also grouped themselves metamerically. This I regard as having taken place as follows: In the gradual increase of thickness and firmness of the skin, or perhaps merely from the secretion of a cuticula of little elasticity; and again in consequence of serpentine swimming movements, circular furrows were formed upon the surface, where the integument was thinner. The sexual follicles, swelling at maturity, and so distending the body at equal intervals, would predetermine definite places for occurrence of these furrows,—that is, between two successive pairs of sexual glands. In the segmented body-zones thus marked out each somewhat centrally placed pair of the remaining organs acquired greater perfection, and thus rendered all its homologues superfluous in its segment, so that these gradually underwent complete degeneration. This, in my opinion, was the origin of metamerism.⁶

The cavities of the parenchyma probably first united into a large sinus about the intestine, from which lymph penetrated into the interior of the paired metameric sexual glands to nourish the developing sexual products floating in them. As this increased in quantity the follicular cavities expanded more and more, and in this way became transformed into the secondary body-cavity with its paired, segmentally arranged chambers. In the epithelial walls only certain areas, subsequently the sexual glands proper

⁶ While writing this the recent "*Lehrbuch der vergleichenden Entwicklungsgeschichte der Wirbellosen Tiere*" of E. Korschelt and K. Heider came into my hands, and in it also the idea is advanced that "by terminal growth first an elongated, non-segmented ancestral form was reached, and then the entire body divided up simultaneously into a large number of segments by a rearrangement of the separate organs." In their opinion, also, the "serpentine motions" gave rise to such a process, since they must have led to the formation in the body of "alternating regions of greater and less mobility."

of the Annelid, retained the ability to produce egg or sperm mother cells; while the remainder, at first a sort of indifferent follicular epithelium, was pressed against the internal organs and tissues, and finally surrounded them in the form of a peritoneum. In this process the hæmal and neural mesenteries and the septa came into existence, as the previously existing dorso-ventral parenchym muscles became enclosed between the median walls of a pair of segmental cavities, and between the anterior and posterior walls of two successive ones.

The greater part of the primary body-cavity, consisting in the ancestral forms presumably of a lymph system of irregular holes and clefts in the parenchyma, was filled up for the most part by the expansion of the sexual follicles. Only a small part of it remained as the definitive vascular system. Since the coelom sacs at first were rounded, they would not apply their walls immediately to the entire surface of the intestine, skin and to one another, but would leave open certain definite spaces,—namely, intersegmental circular spaces, lying transversely beneath the integument; a median space above and below the intestine, communicating each with the circular space, and lying between the right and left lamellæ of the mesentery. Joined to these there was also the above-mentioned intestinal sinus. Thus the method of origin of the segmented secondary body-cavity depicted above would at the same time have led to the formation of the chief portions of the vascular system, as a naturally resulting consequence of the given spacial relations.

Among the peritoneal structures of the Annelids, the neural and hæmal longitudinal muscles require special attention from the difficulty of divining the causes of their first appearance. I have formed the following as yet very hypothetical conceptions of these causes. Part of the non-reproductive elements of the wall of the sexual gland I regard as epithelio-muscle cells, the bodies of which were in the epithelial layer of the follicle wall, while the distal parts elongated as fibrils at each end and tangential to the surface of the gland, when contracting exercised pressure upon the contents of the follicle cavity (were thus functional originally in the discharge of the sexual products). After the

follicle walls had applied themselves to the integument and to the intestine, and had adhered to them, these follicle-muscles could no longer function as such, and disappeared, except in the familiar longitudinal areas on the external body-wall, where they at first strengthened the primary longitudinal musculature, and later entirely supplanted it.

Thus in the perfected organization of the Annelids we would look in vain for a primary longitudinal trunk musculature (perhaps excepting the Hirudinea); but, on the other hand, all the muscles arising from the embryonic mesenchym, as enumerated above, are to be regarded as handed down, with corresponding changes, from the parenchymatous ancestors. In this category belong the transverse muscles, so characteristic of the Annelids, and which are specially well developed in good swimmers. They may have moved from the intraseptal muscle region into the segmental cavity in a horizontal direction to increase the swimming movements, and have thus brought about a subdivision of the coelom into intestinal and nephridial or lateral chambers.⁷

From the parenchym also arises the retroperitoneal connective tissue, which, though occurring in Annelids in only small quantity, in some cases has a truly parenchymatous character, as cartilage-like supporting tissue. In addition, also, the blood corpuscles⁸ in the blood vessels are a remnant of the primitive body-cavity.

The excretory system of the Platyhelminths is commonly regarded as belonging to the parenchym. Scarcely any one doubts that the larval nephridia of the Annelids are homologous to part of that system. I would also derive the definite nephridia, as has been variously done already, from these Turbellarian organs. In this I am guided chiefly by the occurrence of segmentally arranged primary nephridia in many larvæ (two pairs in *Polygordius*, five pairs in *Nereis* and *Dinophilus*), as well as

⁷ Since, to all appearances, the so-called protovertebræ of the Vertebrates correspond to the lateral chambers of the Annelids, we would have to refer their ultimate origin to the mode of swimming in the Annelid ancestor, to the formation of these specific, transverse swimming muscles.

⁸ Morphologically opposed to these proper blood corpuscles are the lymph corpuscles in the coelom, which, arising from the peritoneum, form, to a certain extent, secondary leucocytes, and are possibly related to the sexual products, somewhat as the cellular products of the yolk glands in the Platyhelminths.

by the undoubtedly separate origin of the middle excretory portion of the permanent organ (as in *Psygmobranchus*), which does not come from the peritoneum. It is to be especially emphasized that I would leave entirely out of the question the statements regarding the occurrence of longitudinal canals in Annelids: that concerning *Polygordius* as not confirmed by any of the subsequent studies, and my own concerning *Lanice* as being much more likely a secondary than a primitive condition, contrary to my former unpublished opinion. Yet for my part I still believe, in spite of the criticism of this conception by Berg, with its quite unnecessary and unbecoming additions, that the nephridial tubes are to be regarded as parts of a pair of longitudinal canals, such as the Turbellarians have; in which, in consequence of intersegmental constriction of the body, the excreted fluid was checked, and first gave rise to segmentally arranged openings, after which an ultimate division into segmented sections could take place. To the canals, that were primitively closed internally and provided with fine side branches and end cells, were added in Annelids new structures in the shape of peritoneal funnels. Thence the mode of action of the organ gradually, though not radically, changed considerably, and the entire original terminal portion quite disappeared, as being superfluous. Regarding the original signification of the nephridial funnels, we must bear in mind that the segmentation of the primitively uniform pair of sexual glands must give rise to a corresponding number of paired discharging channels for the sexual products. As in Nemerteans, these could appear as centrifugal outgrowths of the follicle wall, and in many cases they may have met the metameric nephridial tubes (instead of reaching the skin directly), have joined to them so that eggs and sperm were discharged from the body, and thus have been transformed into nephridial funnels.⁹

⁹ Berg formerly expressed the opinion that the definitive nephridia of Annelids were the canals for the sexual products, and arose originally from the walls of the sexual follicles. In my opinion, this idea is justified only in the above restricted form,—only in reference to the nephridial funnels. Moreover, Berg in accepting Kleinenberg's conception of the mesoderm should, consistently, have given up that opinion, since according to Kleinenberg there are no mesodermal somites comparable to the Nemertean gonads. Yet he affirms that he has retained his opinion of the Annelid nephridium unchanged. An explanation seems necessary!

As regards the ectodermal structures, I wish to be as brief as possible here, and to postpone their more particular consideration to my more detailed publication.

In my opinion, the permanent nervous system of the Annelids is undoubtedly to be derived quite directly from the condition found in the Turbellarians. We are to assume here that in the parenchymatous ancestor, probably, the fusion of ganglia around sense organs to make up the chief centers (as shown in the ontogeny of Annelids) had already been completed. I regard the entire larval system, including the ring nerve of the ciliated band and its ganglia, as a special modification of a still older, originally diffuse, subcutaneous nerve-cell plexus. In accordance with this, the ciliated band would not at all have the significance which has been often ascribed to it, but, like the larval form itself, would be only a secondarily acquired peculiarity of an embryo forced into a pelagic life.

The setæ are characteristic of the Annelids; but even in the Turbellaria similar, though quite superficial, skin formations occur, as for example in the *Enantia spinifera* described by V. Graff. From such dermal armament, at first irregularly distributed, may have arisen the true Chætopodia. And here it is to be noted that in *Enantia* the cuticular hooks occur laterally upon the entire margin of the body, with the sole exception of the head region, just as the Chætopodia are confined strictly to the trunk of the Annelid.

We may regard the head tentacles and trunk cirri as having arisen as evaginations of specially sensitive regions of the integument; and since vascular loops were drawn into such hollow processes, they became capable of serving at the same time as respiratory organs for the body. The fact that in the trunk the dorsal cirri, or some of them, became true dorsal branchiæ had its origin in that these were least exposed to injury in occasional movements of the worm upon solid substances, and thus admitted of a thinning of the integument necessary for respiration. The ventral processes came much more into contact with the substratum, and hence became the bearers of an increased sense of touch.

In the digestive tract it is especially the origin of the pharyngeal apparatus that seems to require explanation; but even here the matter is pretty simple if we regard this as an originally circular evaginable part of the foregut epithelium, provided with radiating muscle cells and covered by circular and longitudinal muscle layers, much as we still find in Annelids. Such a condition may without difficulty be derived from the Turbellarian pharynx. But the armament of teeth and their retraction into special sacs of the pharynx are doubtless acquisitions of a later period in the phylogenetic history of our worm.

But little is to be said concerning the phylogenetic development of the remaining regions of the digestive tract; yet this much is probable, that the Turbellarian-like ancestor of the Annelids had no such branched intestine as the present Planarians, which have acquired it along with the flattening and broadening of the body, but had a simple intestinal tube, as in the Nemerteans, ending posteriorly in an anus.

As a direct corollary from the history of the Annelid body, given here in its general outlines, there results a very definite conception of the morphological signification of the mesoderm, as I have already stated in my above-mentioned communication.

Thus, if in Annelids the peritoneal sacs, with all their derivatives, as well as the segmental cavities in them, are to be derived from the sexual glands of their ancestors, then their stages of development in ontogeny, the mesoderm somites and mesoderm-bands, and finally, to be consistent, also in general the secondary or coelomic mesoderm of all Metazoa which have it, must have the original signification of a sexual tissue or of gonads.¹⁰

¹⁰ One of the best evidences would be furnished by a case in which the secondary mesoderm was entirely devoted to the formation of the sexual glands of the adult animal. Such a case seems actually presented, according to the account of S. F. Harmer, in the male of *Dinophilus tenuatus*, a new species of these creatures resembling Annelid larvæ. Here two solid cell-bands in the primary body-cavity, comparable to the mesoderm-bands, are transformed into the anteriorly bifurcated testes, the large cavity of which the author quite justly regards as homologous with the secondary body-cavity of Annelids. On the other hand, the statement of Kleinenberg that the sexual glands in *Lopadorhynchus* arise directly from the ectoderm by invagination, would furnish very strong evidence on the other side; yet I have convinced myself by my own observations upon the same animal that there is an error here, and that the organs mentioned are formed as usual from the peritoneum.

Yet how can structures have the same phylogenetic origin when they, to all appearances, arise now from the ectoderm, now from the entoderm? The ingenious idea of Kleinenberg, that "the sexual cells do not come from the germ layers," will help us out of this difficulty when properly applied. He says further "that they already existed in the ancestors of the Cœlenterates when composed of loosely arranged similar cells, not yet differentiated into ectoderm and entoderm." I would here replace "Cœlenterate" by "Metazoa," since I cannot regard these radiate creatures as the ancestors of the Bilateralia, but only as animals in which the structure of the body has undergone this special transformation, owing to a previous sedentary mode of life. This, indeed, may well have been the case in all animals with radiate symmetry.

Such primary germ-cells would then have originally formed the origin of the secondary or cœlomic mesoderm, and hence belong as little to one as to the other of the two primary germ layers, but are merely interpolated for a time amongst the elements of one layer or the other in the beginning of ontogeny in the Metazoa. Only we are, however, not able to distinguish them from their neighboring cells. So that it does not signify if they subsequently move into the primary body-cavity as "pole-cells," or temporarily remaining in their first surroundings, furnish cell masses growing into the blastocœl, or else by multiplying in situ form epithelial surfaces that subsequently become completely separated.¹¹ Thus, as far as the cœlomic mesoderm is concerned, the discussion as to its ectodermal or entodermal origin becomes quite unnecessary. Since the primary germ-cells probably lay on the boundary between the outer and inner layers, where they obtained both favorable conditions of nutrition and the possibility of discharging their derivatives by the shortest route, they could, later on, get into the ectoderm as easily as into the entoderm.

¹¹ By a similar method Rabl has recently shown how the cœlomic diverticula of the archenteron may be referred to the germ-bands that arise from pole-cells. Whether his "numerical law" is applicable or not, he has thus given a valuable explanation of the apparently different modes of development of such structures; but he is in error when he thinks he can show that the mesoderm universally takes its origin from the entoderm.

We still have the consideration of the question as to the original significance of the embryonic mesenchym. Here again, as it seems to me, the development of the Annelids will help us into the right track,—especially that method of formation of the primary mesoderm which is found in *Lopadorhynchus* and many other Annelids. The paired rudiment on both sides of the anus in the ectoderm represents, according to Kleinenberg, the chief neuro-muscle origin for the ventral band and the permanent mesodermal structures, but contains, as I think, two different, though closely compressed, formative centres,—that of the permanent trunk nervous system, and that of the secondary mesoderm. There are here, in addition, a series of regions in the ectoderm (considered as “neuro-muscle Anlagen” by Kleinenberg) that, in my opinion, furnish the mesenchym, represented in this special case, to be sure, only by mesenchym muscles. In investigating *Lopadorhynchus* larvæ I found, however, more of such mesenchym “anlagen” than my predecessor, and as a rule lying in the regions where the elements arising from them subsequently are attached as muscles to the ectoderm.

This discovery, and the circumstance that in other forms there arise from the mesenchym, in addition to the muscles, connective tissue, the larval and parts of the definitive excretory organs, as well as the migrating cells of the primary body-cavity (primary leucocytes), and probably also the true blood corpuscles, that such migratory cells (as in the Echinoderms) may be formed also from the entoderm, suggests the conclusion that morphologically the embryonic mesenchym is not a uniform structure, but represents rather the sum of the undifferentiated “Anlagen” of very various organs and tissues, which originally arose quite independently from the ectoderm or entoderm, and wherever necessary.

It is not as easy to explain the origin of mesenchym structures by the migration in many cases of cells from the embryonic cœlomic epithelium. In such cases we might assume that the various constituents of the mesoderm had united in a common origin. Then in cases where the entire mesoderm is formed by evagination, or through outgrowths of one or both germ layers, the mesenchymatous and cœlomic embryonic elements may be

simply mixed with one another. But where its rudiment is represented by a single pair of pole-cells these must be regarded as blastomeres precociously removed into the blastocœl, and containing in themselves the future sources of the primary and secondary mesoderm, still unseparated. Since the mesenchym has here and there its own pole-cells,—for we must regard as such the nephroblasts of Whitman and Wilson, and the lateral teloblasts of some Hirudinea and Oligochæta according to the later observations of Berg upon the Lumbricidæ,—those mesoderm pole-cells that later give rise to both primary and secondary mesoderm may have been at one time blastomeres, which by division gave rise to the pole-cells of the cœlomic mesoderm, as well as to mesenchym pole-cells, but which later no longer divided.

The above very sketchy presentation of my views of the mesoderm may be summed up as follows: As in Kleinenberg's theory, the entire mesoderm is not to be regarded as a uniform structure of equal significance with the two primary germ layers, but as a combination of "Anlagen" of very diverse organs that arose at one time entirely independently of one another. But an important element of it, the so-called secondary cœlomic mesoderm, or the genito-peritoneal embryonic tissue, as I would call it, has, as contrasted with the embryonic mesenchym, the significance of a primitive organ,—namely, of an ancestral sexual or gonad tissue that arose from the primary sexual cells, belonging to neither germ layer, in the oldest many-celled animals.

Warsaw, April, 1890.